FURTHER STUDIES OF THE AGGREGATING BEHAVIOR OF AMEIURUS MELAS [1]

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The investigations here reported are continuations of work on the rôle of the sense organs in aggregations of young catfishes (Bowen, 1931), and were directed toward securing further evidence concerning (*a*) the analysis of the factor concerned in the touch reaction; (*b*) the retention of touch and visual aggregating reflexes during prolonged isolation; and (*c*) the influence of aggregation and of isolation upon the physiological processes indicated by the rate of oxygen consumption. Taken as a whole, these studies together with those previously reported contribute to our understanding of the mechanisms concerned in the schooling behavior of *Ameiurus melas* in particular and to some extent to that of fishes in general.

Sense Organs Involved in the Touch Reaction

The reactions of aggregating young catfishes of the species *Ameiurus melas* have already been studied to determine which sense organs are responsible for receiving the stimuli that result in the formation of the aggregations (Bowen, 1931). Vision was found to be essential for the reactions concerned since blinded fishes did not aggregate and normal fishes failed to aggregate in the dark. There were indications, however, that responses to touch are also of great importance, and that the resulting stimulus may perhaps be the fundamental cause of the aggregations and that vision serves only as a means by which the fishes find one another. Individuals of this species are strongly thigmotactic; they always rest with as many points of the body as possible in contact, and in the aggregations they push against each other continually when disturbed. The components of this contact stimulus were not determined, but the early work indicated that it might contain both tactile and gustatory elements. Morphologically this is possible since (Herrick, 1902) the skin of catfishes over the whole body contains not only end organs which are sensitive to pressure but also terminal buds,

corresponding to taste buds in the mouth. These are most abundant on the barblets and diminish in number toward the tail. They are sensitive to chemical stimuli through contact as contrasted with the olfactory organs, which are distance receptors (Parker, 1910).

Observations of the behavior of catfishes in the tanks was also suggestive of a gustatory response. One catfish would often approach another, drag its barblets over it and push against it several times. This occurred to some extent when the second catfish was entirely inactive or when an active individual came in contact with a recently pithed fish. The same positive reaction was also given to goldfishes and mudminnows which were in the same aquarium with the catfishes. The response was negative to a weighted model, made of paraffin mixed with India ink to simulate a small catfish in color and form. The approach was the same as to another catfish, but the barblets were drawn over the model only once and then the fish turned away and swam off.

It was considered desirable to analyze further the contact stimulus which one catfish receives from another, and to determine the relative importance of pressure and of chemical stimulation.

An experiment was designed to determine whether there is a difference in the reactions of a catfish to a scoured stone which presumably gives no chemical stimulus and to another catfish rendered incapable of movement and reciprocal pressure. Fishes were pithed and the wound was covered with melted paraffin to prevent the diffusion of body fluids and a resulting gustatory stimulation. Each of these freshly killed fishes was placed at the side of a crystallizing dish 24 cm. in diameter, and held down by a small pebble since the lifeless bodies floated to the top if unattached. A small stone about the size of a catfish was placed at the opposite side of each dish after which a normal individual about 3 to 5 cm. long was added. Observations of the positions of the catfishes were made at 5-minute intervals, or in a few cases after a longer period; after each observation the normal fish was disturbed so that the position in the next observation was determined anew. After five series of records had been made the pithed fishes and the stones were interchanged so that a positive reaction to one place due to light or some other factor would not mask the results. In most cases the active fishes had come to rest at the end of 5 minutes, although in a few instances one or more were still active. If a fish was moving within a small area the location was noted; otherwise these cases were not included in the results.

The results are given in Table I(a). It is readily seen that the number of positive reactions to the pithed fish and to the stone are about the same, 24 and 29 respectively, whereas the total number of indifferent

reactions where the fish was resting apart from either one totals 94. This indicates that there is no difference between the reactions to a stone and to a catfish if the latter is rendered inactive. Immediately upon the conclusion of the first series a control was run by removing the pithed fishes from each dish and substituting a normal fish. These results are shown in Table I(b). In 62 per cent of the cases the fishes were resting together as contrasted with 16.3 per cent in Table I(a). Since in these cases a response was recorded for each fish, this is equivalent to 31 per cent positive contacts per fish. The increase over the incidence (16.3 per cent) of positive contacts for fishes isolated with one pithed fish is due to stimulation of a visual nature from the moving partner as well as to reciprocal pushing after the two have met. Even with two stones present in the dish with two fishes (Table I, c), the

TABLE I

Reactions of catfishes to stones and to other catfishes as shown by resting positions

Condition of experiment	No. of fishes	Positive reactions		Indifferent	Total
		Fish	Stone		
a. Normal fish with stone and pithed fish	5	10	10	27	47
	5	4	6	40	50
	5	10	13	27	50
Total	15	24	29	94	147
b. Two normal fishes with stone	10	62	18	20	100
c. Two normal fishes with two stones	20	98	48	54	200

fishes aggregated about as much as in the preceding arrangement where the single stone allowed less possibility of purely indiscriminate contact. In about half of these observations the two fishes were found resting together, an equivalent of 24.5 per cent positive contacts per fish, and a decided increase over the 16.3 per cent in (a) where an inert partner was present.

Since it had been found that catfishes responded negatively to a black paraffin model, it was possible that the small amount of paraffin upon the pithed fish might be preventing a positive reaction to the pithed fish itself. Accordingly the responses to a paraffined and to a non-paraffined stone were compared. An equal number of positive reactions, 24, was given to each object with 88 indifferent responses, so

that it may be concluded that there is no definite reaction to the paraffin itself.

From the above results there is no evidence for a gustatory element in the stimulus which one catfish receives from another. When movement and pressure are eliminated the positive response is given in as many cases to a stone as to a catfish. The gustatory stimulus enters only to produce a negative reaction when some unfavorable chemical is present. Observations upon normal fishes in a dish with untreated paraffin models and similar models mixed with India ink to add color showed that a decidedly negative reaction was given only to the India ink models. To untreated paraffin models the reactions were the same as to an inactive fish. It was impossible to eliminate the sight reflex by using blinded fishes in these experiments, because a blinded fish remains active for long periods without coming to rest near any object; such fishes rest only after long activity and in the absence of recent stimulation.

Effect of Isolation upon Aggregating Behavior

The question as to whether the reactions concerned in catfish aggregations are entirely instinctive and automatic or are in part due to conditioning or at least susceptible to modification by conditioning is of interest in this simple type of social behavior found low in the vertebrate scale. Parr (1927) explained the schooling of pelagic fishes by an assumption of a simple automatic eye reflex which acts in the case of milling to produce a type of behavior with no apparent purpose. Learning among fishes has, however, repeatedly been demonstrated. Thus individuals have been trained to associate a stimulus such as light, color (Hineline, 1927), or direction (Churchill, 1916), with food, or in Goldsmith's work (1914) with the nest; and Triplett, 1901, by separating a perch from minnows by a glass partition, conditioned the perch so that after the removal of the partition it made no attempt to reach the minnows by passing the line where the partition had been. Recently Bull (1929) has shown that *Blennius pholis* can be trained to use the senses of taste and smell in the capture of food, although normally they play no part in this behavior. He has demonstrated that purposive movement in fishes can be explained by a combination of unconditioned and conditioned responses in nature as well as in the laboratory.

Two types of reactions of catfishes to one another had previously been observed (Bowen, 1931). Normally vision is the means by which individuals are enabled to come in contact with one another. In addition blinded fishes, previously grouped, were shown to respond to each other when the skin was intact by turning out of their course toward a passing fish in approximately 50 per cent of the cases where the

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two fishes came within two inches of each other. This reaction is apparently due to vibrations set up by the tail of the passing fish and received by the skin, and which act possibly more or less as a thigmotactic stimulus. This positive response may result only after fishes are blinded, but it serves to bring the fishes momentarily nearer one another, and may therefore be considered as a social response.

If the satisfaction of a thigmotactic response is the fundamental basis of aggregating behavior in catfishes, then it seems possible that both the above types of response might be modified if, through isolation, thigmotactic responses from other fishes were prevented for a time. The first indication that such might be the case was found in work with gradient tanks (Bowen, 1931) in which blinded catfishes, isolated from the group for a week, showed a tendency to stay in the opposite end of the tank from the group of fishes when the latter were separated from the single individual by a wide-meshed wire partition. The observed difference in behavior was statistically significant; at the same time blinded fishes which had been members of a group tended to stay in the end toward the group, although the difference from the controls was not significant with blinded fishes.

To determine whether the response of blinded fishes could be conditioned by isolation, individuals were placed in two-quart jars containing plants and fed regularly for a period of 20 days. They were then placed in groups of five in a porcelain tub and the reactions recorded for 15 minutes. At the conclusion of these observations they were kept grouped for one or more days and tested again as a control to determine whether they gave the normal number (50 per cent) of positive reactions after grouping. In almost all cases a positive reaction was given when two fishes actually touched. The few exceptions occurred when they met with some force and darted back in a negative response. In cases where the fishes passed within two inches of each other without touching, however, a difference between previously isolated and grouped fishes was evident. While the latter gave a total of 27 positive responses, 1 negative and 26 indifferent, showing 50 per cent positive reactions, isolated individuals gave 14 positive, no negative, and 38 indifferent responses with only 27 per cent positive. The difference is, however, actually even greater between the two groups; during the first 9 minutes after grouping of previously isolated fishes there was only one positive response and 30 indifferent ones. During this period there were several positive reactions to contact, which apparently served to overcome the effects of isolation, so that the positive reaction was reëstablished at the end of that time. In fact the positive responses for the next 6 minutes rose to 62 per cent of the total.

From this series it seems evident that the positive responses of blinded fishes to one another are eliminated by isolation, but are reestablished again in a few minutes when the fishes are in the same container and contact may occur. The ease with which the response of blinded fishes to vibrations caused by another fish is broken down and the fact that several minutes are required for its reëstablishment make it seem possible that this is a true conditioned response developed after the fishes are blinded, and in connection with the thigmotactic stimulus. It does not act with enough efficiency to enable the formation of aggregations, as one fish can determine the direction of another fish for only one or two turns and then loses it. In normal individuals vision directs the movements of the fishes toward one another at a greater distance than this stimulus can be felt so that it probably acts very slightly if at all in aggregations of normal fishes.

The effect of isolation upon the aggregating behavior of normal fishes was also tested by a similar series of experiments. Several attempts were made to isolate very young catfishes to determine how readily the normal response might be altered before the characteristic social reactions had become established by long use. But it was impossible to keep the very young fishes alive in the laboratory. They died in large numbers under the best conditions and none survived a spell of hot weather. Therefore most of these results were obtained upon older fishes.

The method employed in recording the reactions of the fishes to one another was similar to that for the blinded fishes except that a distance of about a foot and a half was considered the maximum within which a positive reaction was possible, since normal fishes nearly always react to one another within this distance. In all cases the two or three fishes placed in the experimental tub at one time were aggregating closely in the course of a few minutes, so that reactions were recorded only until this occurred. These were of two types, touch reactions where two fishes came in contact without any observable turning from their course when within visual distance, and sight responses where one of the fishes turned definitely toward the other. When either resulted in typical aggregating behavior it was considered positive; if not, indifferent. Usually a touch stimulus resulted in a positive response but in a few cases, almost always with previously isolated fishes, the first touch response was indifferent, but was followed shortly by a positive response often quite clearly as a result of a sight stimulus.

The results of all the experiments are given in Table II. The effect of isolation upon reactions responsible for aggregations seems to be shown most clearly by the number of indifferent reactions as compared

with the positive sight reactions before aggregation is established. In each case where there were indications of a breakdown of the aggregating behavior, the fishes were kept together for a day and the experiment repeated as a control. Such procedure was necessary for comparison since normal fishes which have been isolated for a long period of time require several days before they become as active or responsive as those from a group, a condition which might affect the proportion of positive reactions.

The isolation of very young fishes for five days (Experiment 1, Table II) gave an indication of a breakdown of the aggregating re-

TABLE II

Summary of reactions of catfishes to one another after isolation

Exp.	Number of fish	Number tested together	Length	Days isolated	Indifferent reactions before positive response			Positive sight reactions before contact
					Sight	Contact	Total	
1.	6	2	1 in.	5	6	1	7	1
1(a).*	6	2	1 in.	0	3	0	3	0
2.	8	2	3–5 in.	38	0	1	1	3
3.	8	2	1.5 in.	52	0	0	0	6
4.	3	3	2 in.	161	4	0	4	0
4(a).* (from Exp. 3)	3	3	2 in.	0	0	1	1	1
5.	12	3	2 in.	161	5	5	10	2
5(a).*	12	3	2 in.	0	1	1	2	5

* In (*a*) of each experiment are the results when the fish were retested after one or more days together.

sponses. In Experiments 2 and 3, where young fishes about six months of age were isolated for between one and two months, the behavior was not modified and was entirely typical of fishes from the group. In Experiments 4 and 5, however, where the individuals were kept isolated for over five months, there was decided evidence for an isolation effect. Under these conditions the fishes isolated for five months gave in all 9 indifferent sight responses and 5 indifferent touch responses as compared with one of each after they had been together for 24 hours. Only 2 positive sight responses were noted before contact occurred as contrasted with 6 in the control. As the sight stimulus still acted in two

cases without a touch stimulus, the former was not completely eliminated, but there seemed to be a decided tendency in that direction.

Whether this sight reflex is instinctive or whether it is established soon after hatching as a conditioned response depending upon the positive thigmotactic reaction is still a question. If instinctive, however, it is apparently subject to change by the conditioning processes involved in isolation if these act for a long enough period of time. Probably also this effect can be produced more readily the younger the fishes. Unfortunately observations on the initial reactions of newly hatched fishes could not be made, hence the obvious and crucial test for the relative amounts of instinctive and conditioned elements in this behavior complex is lacking. However, the evidence indicates that conditioning plays a part in this aggregating behavior.

From a survey of the results obtained to date in the investigation of the reactions responsible for the aggregations of young catfishes, we may conclude that the two senses concerned are sight and contact with taste playing no part in spite of the acuteness of this sense in these animals. Sight is the sense by means of which the fishes normally aggregate and the visual response of catfishes may be an instinctive reaction to one another. Touch, however, probably has the more basic rôle, since the sight response can be diminished somewhat in effectiveness by isolation and is reëstablished by contact. The mutual pressure of the fishes due to pushing seems to give the stimulus which maintains these aggregations.

Respiratory Behavior of Grouped and Isolated Catfishes

It has been shown that grouping has an effect upon the respiratory rate of animals. Thus Allee (1926 and 1927) has found that in land isopods and the brittle starfish, *Ophioderma brevispina,* at least when out of the breeding season, the rate of respiration, as measured by the amount of oxygen consumed, is lower per animal for grouped individuals than for isolated ones for the first few hours. The rate of respiration decreases more rapidly for the isolated animals, however, so that after several hours these are respiring more slowly than the grouped ones. There is evidence that, in the case of the starfishes at least, the opportunity for physical contact afforded by the other individuals present is responsible for the group effects upon respiration and for the longer survival of the individuals composing it. Schuett (1931) has investigated this phase of respiratory behavior among goldfishes, guppies, mudminnows and *Fundulus heteroclitus,* and has obtained results similar

to those of Allee for land isopods and brittle starfishes. In his shorter experiments, which covered usually one to five hours, the group consumed less oxygen per fish than did the isolated individuals. Working independently, I have been able to confirm Schuett's results with goldfishes, the only one of his species tested.

It seemed desirable to determine whether any difference exists between the respiratory rate of isolated and grouped individuals of aggregating young catfishes, especially in view of the part that contact plays in such reactions. Accordingly experiments were run with both normal catfishes and with catfishes which had been blinded several days previously in order to eliminate the important effect of vision upon aggregating behavior.

The method followed the technique of Schuett. Each experiment was performed in parallel with normal and blinded fishes. In each case, four single fishes were placed in individual Erlenmeyer flasks, holding one liter, and four were placed together in a similar flask. The flasks were then arranged parallel to two windows to equalize the normal effect of light upon the behavior of catfishes. The flasks had previously been filled with well water which in most cases had been allowed to stand overnight to come approximately to room temperature and to saturation with air, although in the first experiments air was bubbled through the water. In all of the experiments the oxygen tension of the initial samples varied only between 4.5 and 6.5 cc. per liter of water; in this range the rate of oxygen consumption is independent of the oxygen tension (Schuett and citations). After the introduction of the fish, a layer of heavy mineral oil was poured into the neck of the flasks to prevent gaseous exchange at the surface. By means of glass siphoning tubes kept in the flasks, samples of about 15 cc., known to within 0.05 cc., were withdrawn for analysis for oxygen by the method of Winkler. One sample was taken immediately after the introduction of the animal and a second one one hour later. A control flask without fish was sampled similarly. The external end of the siphon terminated in a piece of rubber tubing closed by a clamp. In the first half of the experiments the siphons reached to the middle of the flasks. In the last ten experiments longer siphons were employed and the water was stirred with the siphon one minute before sampling. No difference was noted in the results with the later modification of the technique. The fishes to be used in these experiments were kept on the experimental table in glass-walled aquaria to avoid excessive stimulation while being transferred to the flasks.

Table III shows the results of the experiments. The total oxygen

consumed by four isolated fishes in each experiment is compared with that consumed by the group. The difference which Schuett and I have found between grouped and isolated non-schooling fishes is not obtained here. In fact, with the normal catfishes the members of groups consumed on the whole more oxygen than did isolated individuals but

TABLE III

Total oxygen consumption for one hour of four grouped and four isolated catfishes, blinded and normal (expressed in cc. oxygen per liter)

| | Normal | | Blinded | |
	Isolated	Group	Isolated	Group
1			.56	.20
2	.79	.81	.40	.57
3			.41	.34
4	1.16	1.03	.80	.63
5	.47	.67	.95	.49
6	.64	.64	.42	.49
7	.62	.66	.67	.51
8	.65	.68	.68	.68
9	.26	.42	.73	1.03
10	1.02	.98	1.12	1.27
11	.80	.74	1.00	1.01
12	.72	1.11	1.29	1.02
13	.40	.70	.56	.72
14	.88	.48	.75	.50
15	.31	.54	.48	.42
16	.88	.55	.93	.51
17	.34	.61	.23	.61
18	.77	.55	.59	.39
19	.39	.50	.54	.36
20	.87	.88	.72	.88
21	.63	.63		
22	.46	.57	.59	.53
23	.48	.45	.69	.86
24	.20	.45	.55	.53
25	.18	.41	.46	.42
	Mean difference 0.05087 cc. more oxygen for groups. Probability 0.2158.		Mean difference 0.05 cc. more oxygen for isolated fishes. Probability 0.2898.	

the difference is not statistically significant. In the case of the blinded fishes the isolated individuals consumed very little more oxygen, but here again the difference is not important. The results of three typical experiments are given in Table IV.

The cause of the discrepancy from Schuett's and my results with goldfishes is not difficult to find, nor do these indifferent results offer

any contradiction to his. With normal catfishes the isolated individuals remain quiet during practically the whole experiment. In the groups, on the other hand, the fishes are in motion most of the time, being stimulated by the presence of the other individuals. Thus the rate of respiration of the grouped fishes is increased and the total is higher than for the isolated fishes. The fact that the difference is no greater probably indicates that if the factor of movement could be eliminated with cat-

TABLE IV

Results of three experiments, showing oxygen consumption of isolated and grouped fishes, blinded and normal

Experiment	Normal		Blinded		Control
	Isolated	Group	Isolated	Group	
18	.23 .09 .18 .27 ——— .77	.55	.19 .16 .07 .17 ——— .59	.39	.04
19	.10 .12 .14 .03 ——— .39	.50	.07 .13 .15 .19 ——— .54	.36	−.04
20	.14 .13 .34 .26 ——— .87	.88	.28 .03 .18 .23 ——— .72	.88	−.06

fishes a lower rate of respiration for the groups would be found than for the singles, in agreement with Schuett's work on goldfishes, where problems connected with relative motion were apparently not involved. With the blinded fishes both isolated and grouped individuals are in motion all the time, as are goldfishes, but more actively so. Here the difference is in the same direction as in the case of goldfishes, but is less and not as consistently positive. This is not surprising with the amount of motion occurring with these blinded fishes.

It was hoped that contact responses which gave as much satisfaction as they apparently do in catfishes might produce a difference in the respir-

atory rate, and that this might serve as a method of determining more accurately the rôle of the different sense organs in the social behavior of these fishes. So far this has not been possible, but the results do indicate an interesting difference between the respiratory rate of schooling and non-schooling fishes; at least in these schooling fishes, such as *Ameiurus melas*, individuals stimulate one another to activity by sight or touch and thus offset or counteract the lower respiratory rate found among groups of non-schooling fishes, so that there is no significant difference in oxygen consumption between grouped and isolated individuals. With blinded fishes it may be that contact stimulation is effective in raising slightly the respiratory rate of the group so that here a significantly lower rate was not obtained.

Summary

Catfishes showed no discrimination by contact between a scoured stone and an inactive catfish, nor between a paraffined and non-paraffined stone, but gave a negative reaction to models of paraffin mixed with India ink.

There is no evidence for a gustatory element in the stimulus which one catfish receives from another. A gustatory stimulus acts only to produce a negative reaction when some unfavorable chemical is present.

The positive responses which blinded catfishes give to one another in passing are eliminated by isolation for 20 days, but reëstablished in a few minutes when the fishes are placed together.

Touch responses by blinded catfishes are positive immediately after isolation when contact is gentle enough to prevent shock.

The reactions of blinded fishes to one another due to a response to water vibrations, may be a conditioned response developed after the loss of eyesight, and is probably not effective among normal fishes.

The sight response of normal fishes to one another was not completely eliminated in all individuals by 161 days of isolation, although it was much less marked. It was reëstablished in the course of a few minutes, usually soon after contact occurred. This sight response may be instinctive but is probably subject to modification by conditioning to some extent at least.

A satisfaction evidently accrues to the catfishes from the mutual contact and pressure of the aggregations, and the importance of the thigmotactic response in these reactions is emphasized by these observations.

A comparison of the respiratory rate of catfishes, both normal and blinded, for a period of one hour gave no significant difference between the grouped and isolated individuals.

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